

Equus burchelli. By Peter Grubb

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***Equus burchelli* (Gray, 1824)**

Burchell's Zebra

- Asinus burchellii* Gray, 1824:247. Type locality Little Klibbolkhoni Fontein, Cape Province, South Africa.
- Equus zebroides* Lesson, 1827:346. A renaming of *burchelli*.
- Equus festivus* Wagner, 1835:216. Type locality "Interior of Cape of Good Hope."
- Hippotigris antiquorum* Hamilton Smith, 1841:327. Type locality Angola.
- H(ippotigris) campestris* Hamilton Smith, 1841:329. A renaming of *burchelli*.
- Equus chapmanni* Layard, 1865:417. Type locality between Zambesi and Botletle rivers, Botswana.
- Equus markhami* Tichomirow, 1878:14. No type locality given.
- Equus mauretanicus* Pomel, 1888:229. Type locality Palikao, Algeria; Pleistocene.
- Equus bohmi* Matschie, 1892:131. Type locality Pangani River, Tanzania.
- Equus tigrinus* Johnston, 1897:292. Type locality "British Central Africa."
- Equus (Hippotigris) foai* Prazák and Trouessart, 1899:350. Type locality Angoniland, north bank of the Zambesi, opposite Tette, Mozambique.
- Equus annectens* Rothschild, 1906:691. Type locality near Fort Jameson, Zambia.
- Hippotigris muansae* Matschie, 1906:235. Type locality near Mwanza, Lake Victoria, Tanzania.
- Equus (Hippotigris) kaufmanni* Matschie, 1912:209. Type locality Caprivi Peak, Namibia.
- Equus borensis* Lönnerberg, 1921:181. Type locality 30 miles east of Bor, Bahr el Jebel, Sudan.
- Equus platycornus* van Hoepen, 1930:4. Type locality Orange Free State, South Africa; Pleistocene.
- Equus simplex* van Hoepen, 1930:5. Type locality Koffiefontein, Orange Free State, South Africa; Pleistocene.
- Equus simplicissimus* van Hoepen, 1930:5. Type locality Koffiefontein, Orange Free State, South Africa; Pleistocene.
- Kraterohippus elongatus* van Hoepen, 1930:8. Type locality Orange Free State, South Africa; Pliocene (?).
- Equus lylei* Dreyer, in Dreyer and Lyle, 1931:30. Type locality Florisbad, South Africa; Pleistocene.
- Equus (Asinus) tabeti* Arambourg, 1970:107. Type locality Constantine, Algeria; Villafranchian.

CONTEXT AND CONTENT. Order Perissodactyla, Family Equidae, Genus *Equus*, in which six to nine Recent species are recognized (see Remarks). The extensive literature pertaining to taxonomy and systematics of *E. burchelli* was reviewed by Ansell (1971), Antonius (1951), Cabrera (1936), Rząśnicki (1951), and St Leger (1932). Six subspecies were recognized by Ansell (1971) and Groves (1974). The synonymy was partly listed by Allen (1939), whereas corrections and additions have been given by Ansell (1971) and Ellerman et al. (1953).

- E. b. antiquorum* (Hamilton Smith, 1841:327), see above (*kaufmanni* Matschie, *simplex* van Hoepen, and *lylei* Dreyer are synonyms).
- E. b. bohmi* Matschie, 1892:131, see above (*muansae* Matschie and *borensis* Lönnerberg are synonyms).
- E. b. burchelli* (Gray, 1824:247), see above (*zebroides* Lesson, *festivus* Wagner, and *campestris* Hamilton Smith are synonyms).
- E. b. chapmanni* Layard, 1865:417, see above (*markhami* Tichomirow is a synonym).
- E. b. crawshayi* De Winton, 1896:319. Type locality Henga, west of Lake Nyasa, Malawi (*tigrinus* Johnston, *foai* Prazák and Trouessart, and *annectens* Rothschild are synonyms).
- E. b. mauretanicus* Pomel, 1888: 229, see above.
- E. b. zambeziensis* Trouessart, 1898:64. Type locality Ngwezi val-

ley, probably between the Ngwezi-Zambesi and Machili-Zambezi confluences, Southern Province, Zambia.

DIAGNOSIS. *Equus burchelli* is a medium-sized, striped equid (height of shoulder 110 to 145 cm, mass 175 to 385 kg).

Extant species of zebra approximate a morphocline, with *E. grevyi* at one extreme, *E. zebra* intermediate in many respects, and *E. burchelli* at the other extreme, particularly in body proportions and details of stripe pattern (Fig. 1). Compared with other species, Burchell's zebra has broad or very broad body stripes. The oblique stripes are particularly broad, commencing about half way along the body; where they run onto the croup, they are parallel with the dorsal stripe. The last vertical and/or first oblique stripes branch dorsally to form a more or less complicated "saddle." Vertical and oblique stripes extend to the midline belly stripe except in the nominal subspecies, and there are supplementary brown shadow stripes in some populations. The oblique stripes and saddle do not meet the dorsal stripe, so that on the hind quarters the latter is usually bordered on each side by a white band, and there are no transverse stripes on the croup. The hair along the dorsal midline is not reversed, as in *E. zebra*, but directed backward. Ears are shorter than in *E. zebra*, but not broad and fringed with long hairs as in *E. grevyi*. Chestnuts are smaller than in *E. zebra*, but not minute as in *E. grevyi*.

The skull of *E. burchelli* (Fig. 2) is characterized by a marked convexity of the forehead, a gentle concavity in the profile of the nose, an obtuse angle between face and braincase, relatively broad zygomatic arches (as in *E. quagga* and *E. zebra*), and a supraoccipital crest as in *E. quagga*, not broadened as in *E. zebra* (Azzaroli, 1966). *E. b. antiquorum* differs from *E. zebra* as follows (Eisenmann and de Giulii, 1974): frontals convex, not flat; width across orbital rims less (not more) than across zygomatic arches; infraorbital bar broader; auditory meatus smaller; choanae shorter and broader; and premaxilla narrowed posteriorly, making a longer suture with maxilla, rather than being sharply truncated.

Details of the wear pattern in the cheekteeth (Churcher and Richardson, 1978; Cooke, 1950) distinguish *E. burchelli* from other African equids (Fig. 3). In the upper jaw the first premolar is more frequently lost relatively early in life. The protocone is larger and forms an elongate oval, with the mesial portion contributing a third of the total length. The hypocone is small and may bulge slightly into the medial valley. The parastyle is obliquely flattened and, with the mesostyle, may be buccally grooved. The parastyle and mesostyle are usually smoothly confluent with the ectoloph. The pli caballine is frequently present in the premolars. The pli hypostyle and plis post fossette are usually present and well developed.

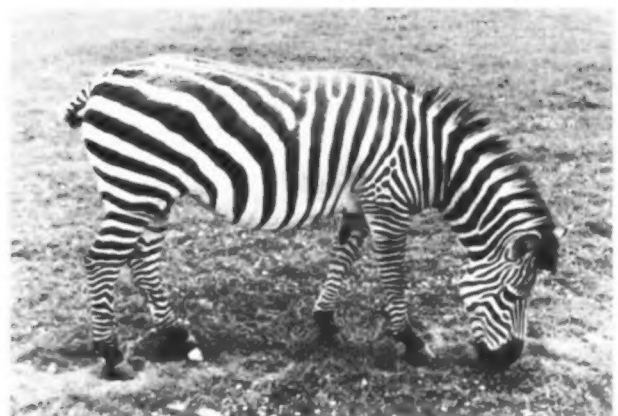


FIGURE 1. Adult female Burchell's zebra, *Equus burchelli bohmi*, from Kenya.

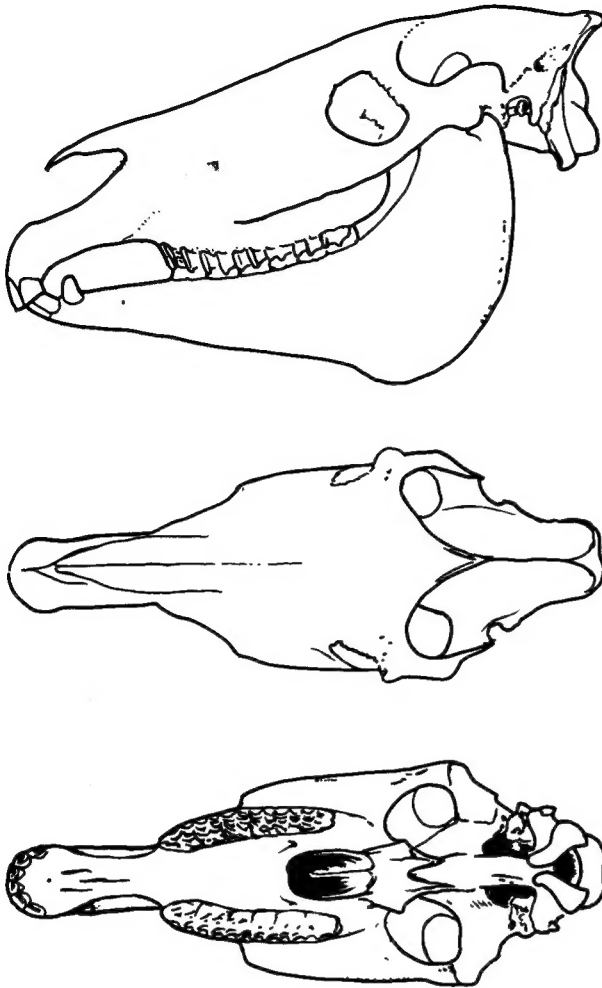


FIGURE 2. Skull of male Burchell's zebra, lacking left canine, from lateral, dorsal and ventral views.

In the lower jaw, the marks or infundibula in the incisors are often absent or less complete than in other living equids. The ptychostylid fold in the hypoconid is small and squared. The metaconid is oval, the metastylid small, pear-shaped and bluntly pointed, and there is some folding of the buccal walls of the entoflexid in unworn teeth.

GENERAL CHARACTERS. The mean mass, in kg, was 247.8 (220.4 to 284.0) in 13 males and 219.1 (175.5 to 241.5) in 8 females from Serengeti (*E. b. boehmi*; Sachs, 1967); 323.3 (277.3 to 357.3) in 8 males, and 322.7 (281.0 to 341.4) in 7 females from east Zambia (*E. b. crawshayi*; Wilson, 1968); 318.5 (267.3 to 373.3) in 57 males and 321.6 (272.6 to 386.9) in 51 females from Kruger National Park (*E. b. antiquorum* or *antiquorum-chapmanni* intergrades; Smuts, 1975a). *E. b. boehmi* is thus lighter, with more sexual dimorphism in mass. Males from Kruger are significantly larger than females only in height of shoulder and girth of neck, where the mean difference is 8.1 cm. Mean height of shoulder, in cm, was 116 (112 to 122) in 13 males and 113 (107 to 121) in 8 females from Serengeti; and 136 (127 to 147) in 57 males, 135 (129 to 141 cm) in 51 females, from Kruger.

Mean basal length of the skull in mm was 444.8 in 16 *E. b. boehmi*; 473.8 in 30 *E. b. chapmanni* and *E. b. antiquorum* (Willoughby, 1974); and 450.5 (414 to 487) in 11 *E. b. burchelli* (Antonius, 1951). These measurements overlap with those for *E. zebra*, which has on average a longer skull, but are outside the range given for the still larger *E. grevyi*.

Burchell's zebra has shorter long bones than Grevy's zebra, though they are of similar diameter. Proportions are more similar to the mountain zebra (*E. zebra*), though the metapodials may be longer in the latter (Arambourg, 1970; McMahon, 1975; Willoughby, 1974). The terminal phalanges and hooves of *E. burchelli* broaden distally as in *E. grevyi*, though they are not as broad as

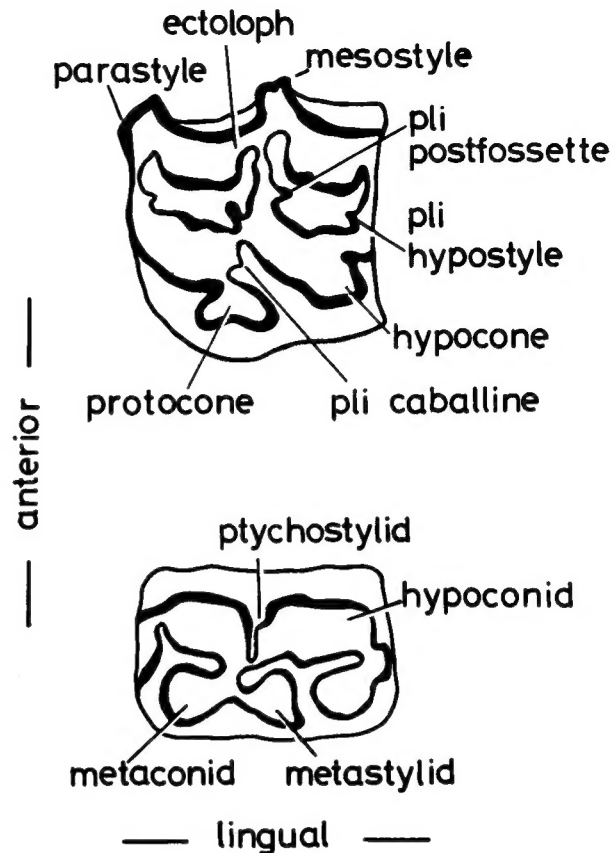


FIGURE 3. Left upper (above) and right lower (below) third premolars of Burchell's zebra, showing features mentioned in the text (modified from Cooke, 1950).

in the horse, quite unlike the abbreviated phalanges and compressed hooves of *E. zebra* (Bourdelle, 1955).

There is a short erect mane and a long black or whitish tail tuft, as in other wild equids. The stripe pattern has been described in detail by Ewart (1899) and Cabrera (1936). Each individual has a unique stripe pattern and this can be used in a key-out identification scheme (Briand Petersen, 1972). Abnormalities in pelage pattern are relatively rare and usually involve anastomoses and broadening of the black stripes, culminating in a black pelage with scattered white spots (Kingdon, 1979).

The color pattern is thought to form as equidistant stripes perpendicular to the dorsal line in the third week of development, earlier than in other zebras (Bard, 1977), while it may have originally evolved from a white-spotted pelage, such as that seen in juvenile tapirs (Pocock, 1909).

There is much geographic variation in the stripe pattern (Fig. 4). Stripes are most numerous and close-spaced, without shadow stripes, in *E. b. crawshayi* of Malawi, southeastern Zambia, and northern Mozambique. They are fewer and more widely spaced in subspecies occurring to the north, northwest and south (Ansell, 1971; Cabrera, 1936). The stripes are broadest, and fewest, only rarely with shadow stripes, in *zambeziensis* and *boehmi*. *E. b. zambeziensis* is distinguished from *E. b. boehmi* by its longer braincase, but so far only six skulls, none topotypical, have been examined (Ansell, 1971; Azzaroli, 1966). Single animals or groups in the northern part of the range of *boehmi* (Sudan, Ethiopia, Somalia, Uganda, Kenya and extreme northern Tanzania) can be maneless, sometimes also lacking the black ear markings (Mohr, 1962). The holotypes of *borensis* (Lönnerberg, 1921), and *isabellae* (Ziccardi, 1959), are maneless.

A cline in stripe pattern extends southward and southwestward from Malawi, in which shadow stripes increase in number and width, while the leg stripes become narrower and begin to disappear, the reduction commencing distally and eventually leading to narrowing and disappearance of stripes on the hind-quarters, belly, and humeral areas. Variation across the cline is to some extent paralleled by variation within local populations. Typically, the legs are striped to the hooves and shadow stripes



FIGURE 4. Skins of Burchell's zebra, from top to bottom of *E. b. boehmi*, *E. b. crawshayi* and *E. b. antiquorum* (from Lydekker, 1912; and Rau, 1978).

are present in *E. b. chapmanni*; the legs are white at least below carpus and tarsus though with a few streaks on the hocks, the body stripes are narrower and the shadow stripes more prominent in *E. b. antiquorum*; the belly, lower haunches and the whole of the legs are white, shadow stripes are present, posterior oblique stripes are reduced, the ground color of the body is buffy rather than white, and anastomoses of main and shadow stripes may occur, in *E. b. burchelli*.

Infundibula are said to be absent from the lower incisors in northern subspecies (*zambeziensis*, *boehmi*, *crawshayi*) but pres-

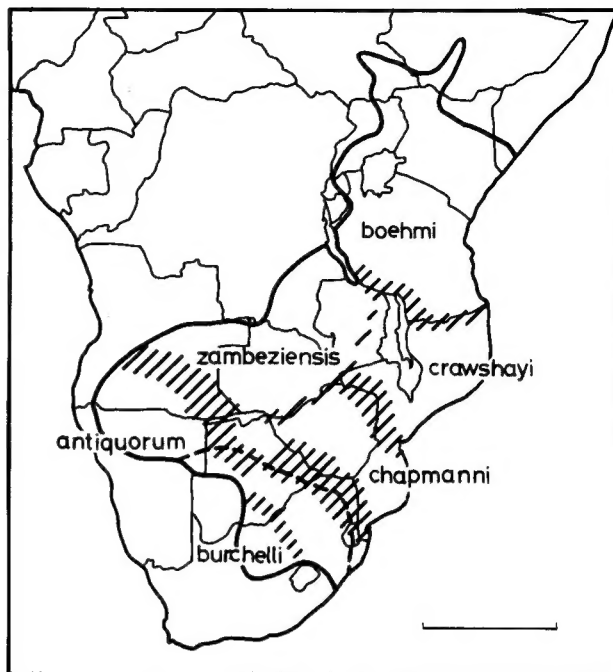


FIGURE 5. Map of Recent distribution of subspecies of Burchell's zebra. The dotted line in southern Africa marks the present southern boundary of the species' range, and the hatched areas represent regions where subspecies are presumed to intergrade (modified from Ansell, 1971). The scale represents 1,000 km.

ent in southern ones (*chapmanni*, *antiquorum*, *burchelli*) (Hoffstetter, 1950). They are usually present, however, in all lower incisors of *E. b. boehmi* (Klingel and Klingel, 1966a) but only in about 50% of specimens, and then only in I_2 and I_3 , of *E. b. antiquorum* (Eisenmann and de Giuli, 1974). Southern subspecies have more upstanding manes, with pronounced forward-curved forelocks (Astley-Maberly, 1960; Groves, 1974), and the tail tuft tends to be fuller, commencing nearer the tail root, and more often white than black. Southern subspecies are taller and appear less compact and "dumpy" than northern ones (Gregory, 1926). All limb bones average longer in *E. b. antiquorum* than in *E. b. boehmi* (Willoughby, 1974).

DISTRIBUTION. Burchell's zebras occur throughout much of the Southern Savanna of Africa, and extend into the Somali Arid Zone up to the 10 inch isohyet (Stewart and Stewart, 1963), and formerly extended into the Southwest Arid Zone up to the 400 mm or 12 inch isohyet (Fig. 5). The distribution (Ansell, 1971) formerly included Namibia south to the Gobabis area, Botswana except the southwest, northeast Cape Province (Mafeking area, between Campbell and the Vaal River, but not south of the Orange River), Transvaal, Orange Free State, south and south-east Angola, Zimbabwe, Mozambique, Zambia, Malawi, south-east Zaire, Tanzania, Rwanda, southern and northeastern Uganda, Kenya except for the northeast, southeast Sudan northwest to about 7° north 30° east, south Somalia, and Ethiopia from the extreme southwest through the Rift Valley to about Lake Zwai.

It is now extinct in the Gobabis area, much of Botswana, Cape Province, Orange Free State, most of Transvaal, Natal except for Zululand, and Mozambique south of latitude 23° south, but it has been reintroduced in Transvaal, Orange Free State and Natal. It has been introduced into the Cape of Good Hope area (Ansell, 1971).

Burchell's zebra is sympatric with Grevy's zebra in Kenya and with the mountain zebra in Namibia and Angola (Antonius, 1951; Keast, 1965). It is said to have been sympatric with the quagga (Groves, 1974), but the evidence was not considered adequate by Rau (1974).

FOSSIL RECORD. Burchell's zebras are known as fossils from the Pleistocene and perhaps the late Pliocene. Churcher and Richardson (1978) mapped the localities from which specimens are recorded, in Namibia, South Africa, Zimbabwe, Zambia, Tanzania and Kenya (all within the present range), and from

Algeria, Morocco, Tunisia, and Mali (*E. b. mauretanicus*), indicating an extension of a Southern Savanna faunal element far north of its present distribution. Its ecological associate, the blue wildebeest, *Connochaetes taurinus*, is also known from North African deposits. Names based on South African fossils of Burchell's zebra are regarded as *nomina vana* by Wells (1959). The identification of both *E. burchelli* and *E. quagga* as fossils in South Africa (Churcher and Richardson, 1978; Cooke, 1950) may require reinterpretation in view of Rau's (1974, 1978) views on the relationships of the two species.

FORM AND FUNCTION. Burchell's zebra is apparently similar to other equids in its anatomy and physiology (Bell, 1971; Klingel, 1969a; Smuts, 1974a, 1975a, 1976a, 1976b), but apart from studies of reproductive physiology and growth, most relevant papers deal with immobilization (Ebedes, 1972, for example) or veterinary care in captivity (Jones, 1976). Comparative hematology data are given by Seal et al. (1977). The mean rectal temperature was 39.3°C (38.4 to 41.8, $n = 13$) immediately after death in shot zebras (Denney, 1969). Leahey (1969) attributed the fat, sleek appearance of the species to the presence of a subcutaneous layer of yellow fat that may act as a food reserve. Demmer (1966) stated that the maximum speed attained was 60 to 70 km/h.

Various often compatible hypotheses have been put forward to explain the function of striping in Burchell's zebra. Insofar as they may show sexual interest in a striped model, zebras apparently recognize the stripe pattern (Grzimek, 1960), and may identify individuals by their unique patterns (Klingel, 1967), so that a visually-based bonding system is formed in zebra societies (Kingdon, 1979). Striping may provide camouflage, as it produces obliterative shading through pattern-blending at a distance (Mottram, 1915) or under suboptimal light conditions. It also creates an optical illusion, making the animals appear larger and creating a confusing effect at close range (Cott, 1940), or making them hard to see when moving (Eloff, 1966). Stripes on the belly break up the white area, perhaps making the animals less visible to tsetse flies (Swynnerton, 1936; Andersson quoted by Eloff, 1966). The rump-pattern of radiating oblique stripes is conspicuous (see photographs in Keast, 1965) and is perhaps analogous to the rump-patch of pronghorn, *Antilocapra americana*, and other ruminants. The white ear tips may contribute to signalling the emotional state of the animal (Matthews, 1969).

The dental formula is I 3/3, C 1/1, P 3-4/3, M 3/3, total 40 or 42. The milk canines of both sexes and the permanent canine, when present in the female, are significantly smaller than the permanent canines of males (Erz, 1964).

ONTOGENY AND REPRODUCTION. The reproductive biology of Burchell's zebra has been thoroughly investigated by King (1965), Klingel (1965a, 1969a), and Smuts (1976a, 1976b). Zebras tend to breed seasonally but the dispersion of birth dates is not as restricted as in other plains ungulates. Though most births are in the wet season, there are births in all months. Of 151 births to marked animals in Ngorongoro, 85% were in October to March and 28% in January alone (Klingel, 1969b). Similar figures are available for Serengeti (Klingel, 1969a) and the Kruger National Park (Smuts, 1976b), where the peak of foaling corresponded closely to the peak in rainfall and was usually in January. Evidence that the main foaling period is outside the rainy season in Zimbabwe and Zambia (Ansell, 1960a; Dasmann and Mossman, 1962b; Dowsett, 1969) is based on relatively few observations.

Male sexual maturity is attained after 4 years (Smuts, 1976a). The adult testis mass is reached at 5 years, with rapid increase after about 3.5 years. Increase in tubule diameter is not as rapid. The testis of adults (5 to 20 years) is 8 to 10 times as large as in 2 year-olds, and the penis is 10 to 15 cm longer. The testes plus epididymides have a mean mass of 302 g (176 to 465, $n = 195$) in adults and a mean of 229 g (100 to 350, $n = 16$) in 4.5 year olds. Spermatozoa may be found in the seminiferous tubules by 2.5 to 3 years, with the first appreciable numbers in smears by 3.5 years. The prepubertal period is longer than in the horse, with first sperm observed at 2 years, and full reproductive capacity and physiological maturity at 4.5 years (Smuts, 1976a). Libido has been shown as early as at 18.5 months (Wackernagel, 1965), before spermatogenesis is complete.

Sexual maturity in the female is at roughly the same age as in the horse (16 to 22 months). Smuts (1976b) gave uterine and vaginal dimensions in relation to age, and a thorough description of the development of the ovaries. The first estrus has been recorded at 13 months (Klingel, 1965a) or 15.5 months (Wackernagel, 1965); the first ovulation at 1.5 and 2 years (Smuts, 1976b).

By 3.25 to 3.5 years ($n = 12$) all females have ovulated (Smuts, 1976b). Age at first conception had a mean of 2 years 4 months (1 year 10 months to 2 years 9 months, $n = 5$; King, 1965). Age at first parturition was 3 years 7 months and 3 years 7.5 months in two captive animals (Wackernagel, 1965); Klingel (1965a) gave a mean of 3.75 years.

Estrus lasts 2 to 9 days, diestrus 17 to 24 days (Wackernagel, 1965). The gestation period had a mean of 371.2 days ($n = 14$; Wackernagel, 1965). Smuts (1976b) gave a single example of 396 days. Treus (1961) estimated gestation at 360 to 375 days, suggesting that male foals have a longer gestation than females. Foal heat (post-partum estrus) occurs 8 to 10 days after birth, followed by either suppression of estrus for up to 16 weeks post-partum or normal estrous cycles, with conception about 4 weeks post-partum, so that the foaling-conception interval is from 2 to 24 weeks ($n = 6$; King, 1965). Lactation can continue for up to 16 months, but if the dam becomes pregnant, it ceases 1 to 2 months prior to parturition (Smuts, 1976b) or at 25 weeks of pregnancy (King, 1965). The udder increases from a range of 0.2 to 0.5 kg to 2.5 kg 35 days before parturition (Smuts, 1976b). King (1965) stated that weaning was at about 7 months, but the earliest recorded by Smuts (1976b) was 11 months.

The shortest foaling intervals observed by Klingel (1965a) were 378 and 385 days. The mean interval was 13.9 months in 14 births of two captives (Wackernagel, 1965). In a total of 120 mares observed over a three year period, 15, 33, 41 and 10% had 3, 2, 1, and 0 foals, respectively (Klingel, 1965a). This apparent foaling periodicity neglects undetected neonatal mortality. The conception rates were 78 and 89% in samples of 236 and 31 mares (Smuts, 1976b) in Kruger National Park. These rates are relatively low compared with other plains game, due to successive conceptions being at least 20 days later each year, and to the reduced probability of conceiving during the dry season.

The female reproductive cycle is synchronized with photoperiod, but there is a marked increase in conceptions during the first spring rains, so that the foaling season may be advanced or delayed. Smuts (1976b) speculated that this was either due to increased quantity and improved quality of fodder, estrogenic pheromones in pastures, or direct stimulus of the central nervous system by the visual pathway.

Mean testis mass in adults changes from 268 g in July to 345 g in January; tubule diameter increases from about 170 μ to 190 μ . Dimensional changes are less marked than in more strictly seasonal breeding species, but are coincident with the sexual activity of the female. There is no month without some spermatogenesis (Smuts, 1976a).

Single births have been described by Klingel and Klingel (1966b) in the wild, and by Wackernagel (1965) in captivity. Births took place with dams on their sides and were completed in 8 and 9 min (Wackernagel's data cited second, when available). Neonates extricated themselves from the birth membranes without aid, stood after 11 and 13 min, stepped after 19, walked after 32, cantered after 44 and 60 min, and suckled after 67 and 71 min. The meconiums were dropped after 97 and 105 min, and the afterbirths soon after parturition or up to 1.5 h later. Dams nibble only a little of the afterbirth. Wackernagel (1965) noted that most births occur in the dark, towards morning, and that the dam apparently eats the foal's feces until 18 to 20 days post-partum. In the wild, other family members ignore births, though the stallion may stay 10 to 50 m away. The dam is protective towards her foal and drives off other adults who approach. Imprinting of the dam on her foal is completed within the first few weeks of life.

Allometric growth in body dimensions and fetal growth curves were presented by Smuts (1975a), who found that height of shoulder reaches the adult range by 1 year. Body mass attains adult values after three years. The eye lens shows little annual increase in mass after 4 years, though the linear relationship between dental age and mass of eye lens is maintained. The large overlap between age groups of mass of eye lens precludes its use as an independent assessment of age (Smuts, 1974a).

The tooth eruption order, replacement sequence, and tooth wear, including the pattern of incisive infundibuli, are much as in the horse and can be used for ageing (Erz, 1964; Klingel, 1965b; Klingel and Klingel, 1966a; Smuts, 1974a). The tooth eruption sequence of the permanent dentition in both upper and lower jaws is M1, M2, I1, P2, P3, P4, I2, C, M3, I3 (Erz, 1964). Klingel and Klingel (1966a) recognized 21 tooth-wear classes (see also Smuts, 1974a). Annual laminae in the cementum of the permanent incisors and molars are relatively clear in zebras from Kruger National Park compared with those in East Africa (Smuts, 1974a). The rate of attrition of the cheek teeth appears to be constant

(Spinage, 1972a) as molar height and tooth-wear class are closely correlated.

ECOLOGY. Burchell's zebra differs from other African savanna ungulates in its behavior, social organization, diet, and breeding schedule. It occurs in more mesic areas than the other African equids (Fig. 5), where water is available, in light woodland, open scrub, grassland, dambos and occasionally broken, hilly ground (Ansell, 1960b; Smithers, 1966, 1971). Zebras show a preference for *Acacia* rather than *Commiphora* woodlands, avoiding dense *Commiphora* woodland completely in the Tarangire Game Reserve, Tanzania (Lamprey, 1963). They range up to 4,400 m on Mt. Kenya, with an altitudinal variation within home ranges of as much as 1,100 m (Coe, 1972). On the edge of their distribution, at Lake Rudolf, they are restricted to a narrow strip of *Sporobolus-Dactyloctenium* grassland along the lake shore (Stewart, 1963).

Grass constitutes over 90% of the zebra's diet, whether assessed by the frequency of stomach-contents fragments in point counts (Gwynne and Bell, 1968) or by spot observations of feeding animals (Lamprey, 1963). There may be some browsing and digging of corms and rhizomes in dry periods (Pienaar, 1963). Between 17 and 20 species of available grasses are taken on the Athi-Kapiti Plains, Kenya, with a greater variety in the dry season (Casebeer and Koss, 1970). Of 40 grass species and 72 non-grass species utilized by ungulates in the Tarangire Game Reserve, the zebra takes 23 and 10 species, respectively, the non-grass species all being herbs (Lamprey, 1963). Zebras show low selectivity compared with kongoni (*Alcelaphus buselaphus cokei*) or wildebeest in the Athi-Kapiti Plains, though elsewhere (Tarangire) the ranges of species taken by zebras and by wildebeest are very similar. Comparisons between representation of plant species in the field and in fecal contents indicate that favored species include *Themeda triandra*, *Cynodon dactylon*, *Eragrostis superba* and *Cenchrus ciliaris*, whereas *Pennisetum mezianum* and *Digitaria macroblephara* are among species selected against (Casebeer and Koss, 1970; Lamprey, 1963; Stewart and Stewart 1970).

In the Serengeti the diet of zebras consists mostly of fibrous plant parts, especially in the dry season (Bell, 1971). Proportions of grass leaves, sheaths, and stems in counts of stomach-contents fragments were 37, 44 and 15%, respectively, in the wet season, and 2, 49 and 51% in the dry season in samples from Serengeti zebras (Gwynne and Bell, 1968). Zebras tend to be the first to move in the grazing succession, opening up the herb layer, altering the stem/leaf ratio in the pasture, and making use of different strata in the herb layer from the wildebeest and other ruminants. By analogy with horses, zebras are inferred to be 66% as efficient as domestic cattle in extracting protein, but their passage time is twice as fast. The rate of assimilation is hence 133% of that of cattle, so they can support themselves on a diet too low in protein to sustain ruminants (Bell, 1970, 1971). Food is cropped by the incisors rather than plucked (as in ruminants). The diet in general is less selective, has the lowest protein content, and is composed of the toughest, most abundant, and most accessible plants or plant parts. Yet the Burchell's zebra is not as abundant as the wildebeest on the Serengeti.

At least in that region, zebras feed on short grass at the tops of catenas, as the rains commence, and move down the catenary slope towards longer grass in the dry season. They also migrate from areas of low rainfall to areas of high rainfall over the season, though their migration is not as spectacular as that of the blue wildebeest (Bell, 1970, 1971). Zebra associate with other ungulates, but particularly wildebeest. Coefficients of interspecific association are positive and show peaks in the late wet season (descent of the catena) and at the end of the dry season (return to the top of the catena) (Bell, 1970).

Zebra populations can be sedentary, with high population densities and small ranges, or migratory, with relatively low densities and different wet and dry season home ranges of great extent. The sedentary population in Ngorongoro, Tanzania, has a population density of 19.2/km² (Turner and Watson, 1964) and group home ranges of 80 to 250 km² (Klingel, 1969a). Densities range from 0.7 to 2.2/km² and home ranges from 49 to 566 km² (mean 164 km²) in the Kruger National Park where both sedentary and migratory populations occur (Smuts, 1975b). The numbers of the largest migratory population, from the Serengeti Plain, Tanzania, are estimated to be between 57,000 and 280,000 (Grzimek and Grzimek, 1960a, 1960b; Hendrichs, 1970; Kruuk, 1972; Schaller, 1972; Talbot and Stewart, 1964). Length of the migratory route is between 100 and 150 km. Population density is about 9.5/km² (Kruuk, 1972) and home range 300 to 400 km² in the rainy

season and 400 to 600 km² in the dry season (Klingel, 1969b). Migratory populations are also known from Ethiopia (Urban and Brown, 1968) and Namibia (Smuts, 1974b).

There is a daily cycle of movement from sleeping grounds in open areas with short grass cover, to grazing grounds (Klingel, 1969b).

Sex ratios at birth are not significantly different from 1:1 (Klingel, 1965a; Smuts, 1976c; Wackernagel, 1965). Population sex ratios, expressed as females/male, range from 0.92 (Dasmann and Mossman, 1962a) to 3.32 (Foster and Kearney, 1967). Smuts (1976a) gave the following sex ratios for the Kruger National Park and for the Loliondo area, Tanzania: embryos and fetuses, 0.90, 1.08; birth to one year, 1.27, 1.22; 1 to 2 years, 0.91, 1.00; 2 to 3 years, 1.09, 0.96; 3 years and over, 1.32, 1.78. Predation distorts the sex ratio; it is near unity where predation is reduced.

Approximate time-specific life tables constructed from the age distribution of skulls recovered from predator kills in the Akagera (Monfort and Monfort, 1978; Spinage, 1972a) and Kruger National Parks (Smuts, 1976c) show that mortality rate increases with age, being less than 20% annually for zebras under 10 years of age, and over 20% in older animals. Mean length of life was given as 9.7 years for males and 8.5 for females (Spinage, 1927b). Animals survive into the 18 to 20 years age group; the maximum ecological longevity is 21 years (Smuts, 1976a, 1976c). Life spans of over 28 years (Flower, 1931) and 40 years (Weber, 1942) have been recorded in captive animals.

Because not all mares foal in a given season and there is some neonatal mortality, it is inaccurate to estimate either conception rate or juvenile mortality from counts of mares with or without accompanying foals. Smuts (1976b) estimated the conception rate to be 79% from post-mortem examination of mares from Kruger National Park, although Kruuk (1972) quoted Skoog as saying that all fully adult mares he examined in the Serengeti were pregnant. Mortality of young in their first year was 17.9 and 19.6% for males and females, respectively (Spinage, 1972b), but these estimates, from the Akagera National Park, are probably much too low. Schaller (1972) interpreted Klingel's (1969b) data as implying that two-thirds of the foals disappear within the first few months of life, but Klingel (1969b) himself stated that post-natal mortality in the Ngorongoro Crater could not be evaluated. One hundred and twenty mares produced 184 foals over 3 years, giving an apparent conception rate of 51%, but neonatal mortality was probably also involved. By observing seasonal changes in the proportions of mares with foals in the Serengeti population, Klingel (1969b) estimated that juvenile mortality in the first year is 30%, excluding immediate post-natal mortality. The proportions of dams with surviving foals at the end of the breeding season reflected both conception rate and first-year mortality, and were correlated with precipitation in the following series: Ngorongoro, 48%; Serengeti, 31%; Kruger, 27%; Wankie, 15%; and Etosha, 14%; mean annual precipitation was 908, 773, 617, 590, and 323 mm, respectively (Klingel, 1969b). Thus, juvenile mortality is possibly between 50 and 80% in the first year, but regional variation in conception rate, if it occurs, may complicate the picture.

Predators tend to kill more males than females. Sex ratios in kills, expressed as the number of females killed per male, were 0.54 in the Serengeti-Mara (n = 818) and 0.48 in Kruger (n = 138; Smuts, 1976a). But zebras may be killed by lions (*Panthera leo*) in the expected sex ratio (0.83; n = 138) in the Serengeti (Schaller, 1972), whereas spotted hyenas (*Crocuta crocuta*) tend to kill relatively more females in Ngorongoro (Kruuk, 1972) where the ratio was 2.25 (n = 55). The lion is the principal predator of zebras. They constitute 15.8% of prey in Kruger (n = 12,223; Pienaar, 1969), and 22% in the Serengeti (n = 887), where zebras and wildebeest are present in the ratio 1:3 yet are killed in the ratio 1:1.75 (Schaller, 1972). Zebras are probably selected because they are less migratory and hence more available as potential prey.

Spotted hyenas are also significant predators in Ngorongoro and Serengeti, where zebras make up 15% of kills (n = 465; Kruuk, 1972), but not in Kruger (Pienaar, 1969). Zebras constitute no more than 6% of prey items for other predatory species. Hyenas, cheetahs (*Acinonyx jubatus*), and wild dogs (*Lycaon pictus*) take more foals than do lions.

If zebras are pursued for too long in a vehicle, they suffer from acidemia and myopathy (Harthorn and Young, 1974, 1976; Harthorn et al., 1974; Hofmeyr and Louw, 1973), but it has yet to be established whether this phenomenon is significant in pursuit and capture by natural predators.

The literature on zebra endoparasites was documented by Karstad (1979); endoparasites from southern African zebras were listed by Neitz (1965), and individual parasite loads were dis-

cussed by Pester and Laurence (1974). Organisms parasitic on Burchell's zebras include African horse sickness virus, for which the zebra is a reservoir, anthrax (*Bacillus anthracis*), *Trypanosoma* spp., other protozoans such as *Babesia* (Brocklesby and Vidler, 1965; Dennig, 1965), and *Toxoplasma* (Riemann et al., 1975), trematodes including amphistomes and *Schistosoma* (Pitchford, 1977), at least three species of cestodes, up to eleven species of nematodes, including filarian worms (*Setaria*), lung-worms (*Dictyocaula*), and hook worms (*Strongylus*). Bot larvae (*Gasterophilidae*) infesting Burchell's zebras include *Gasterophilus ternicinctus*, *G. pecorus* and *G. inermis* in the cardiac stomach, *G. nasalalis* and *G. meridionalis* in the pyloric stomach, and *G. haemorrhoidalis* in the rectum (Howard, pers. comm.; Pester and Laurence, 1974; Zumpt, 1965). Nostril fly larvae (*Rhinoestrus*) of at least three species may be present in the nasal cavity. Lice (*Haematopinus*) are known from the juvenile pelage, and there are at least nine species of ticks recorded from Burchell's zebras.

The endoparasitic load is often very heavy, with high levels of trichostrongyle and oxyurid nematode, cestode, and amphistome trematode infestations in the digestive tract, and worm nodules in the liver; yet the animals appear healthy. The role of trypanosomes is not entirely clear. Kluge (1945) could find no trypanosomes in the blood of 18 healthy zebras from Zululand. Weitz and Glasgow (1956) record no evidence of zebras being bitten by the vector, *Glossina* (tsetse), in examination of over 1,200 blood meals of *Glossina* from Zambia, Tanzania, Kenya, and Uganda. Symes and McMahon (1937) obtained similar results from over 3,000 blood meals from a single locality in northern Tanzania. Unlike the horse, the zebra appears to be remarkably free from tsetse bites and hence from trypanosomiasis. McCulloch (1967), however, reported trypanosomes of the *brucei* subgroup in two zebras in poor condition and with abnormal behavior, indicating neurological disturbance, from the Grumeti game controlled area, Tanzania.

BEHAVIOR. Six calls were recorded by Klingel (1967): a two-syllable alarm call made on sighting predators; a loud snort when moving into potentially dangerous cover; a long drawn-out snort of contentment; a short high-pitched squeal from males when bitten or hurt; a long drawn-out wail from a foal in distress; and the species-characteristic contact call of inspiration-expiration: a-ha, a-ha, a-ha, the first "a" higher in pitch (Rzǎśnicki, 1951), or kwa-ha, kwa-ha, kwa-ha ha ha (Astley-Maberley, 1960).

There are two chief facial expressions—threat (with ears down) and greeting (ears up and directed forwards). Increased intensity in both cases is expressed by opening of the corners of the mouth, and by chewing movements. "Rossigkeitgesicht" (estrous face), accompanying presenting or lordosis, may have originated from precopulatory combat, as it resembles a strongly-expressed threat-face (Antonius, 1937; Trumler, 1959a), or it may be a vestige of grooming (Kingdon, 1979).

Self-grooming in Burchell's zebra is like that of other equids (Trumler, 1959b). Allogrooming is frequent in the species, its relative frequency declining in the following series: mares and youngest foals; mares and next youngest foals; stallions and mares or foals. Grooming zebras usually stand side by side, head to tail. There is some tendency for males to groom certain females preferentially. Conversely, males may selectively attack particular individual females, at least in captivity (Lang, 1972).

Social organization was studied by Klingel (1965a, 1967, 1969b). There are two kinds of social groups: family groups (stallion, mares and their foals) and stallion groups (males only, including solitary males). Of 1,689 family groups in the Kruger National Park there were only three cases of mares on their own (Smuts, 1976a). There is no social organization above the level of groups, though Smuts (1976c) found that stallion groups associate preferentially.

Family groups are stable. The youngest family stallions were 5 to 6 years of age in Ngorongoro (Klingel, 1969b), but in the Kruger National Park, some family stallions were younger (Smuts, 1976c). If the group stallion dies or disappears, another male replaces him. With their first estrus, young females are abducted by males of other family-groups or stallion groups, the latter thus founding new families. In her first estrus, the female stands with legs apart and tail lifted in an estrous posture which attracts up to 18 males. The family stallion is rarely able to keep her. Only 1 out of 44 females in the abductable age-group remained with her own family in Ngorongoro. There may be several abductions with successive estrous cycles. As females mature, the estrous stance becomes less conspicuous and confined to the

period immediately before mounting, so without the optically conspicuous stance, there is no competition for mature mares.

A rival male may attempt to drive off the family stallion (Estes, 1967). If the stallion leaves the family, his sons may follow him. Young males normally leave the family at 1 to 3 years of age, and exceptionally up to 4.5 years. Smuts (1976a) recorded the earliest departure as 9 months. Bonds with the mother are lost when she has a new foal and as opportunities for play-fights with other males are greater in stallion groups. Family stallions nevertheless do not show antagonism to their sons. Mature adult females only exceptionally leave families.

Zebra social groups are non-territorial and have overlapping home ranges but females are antagonistic towards those in other groups. Family stallions greet other males in the vicinity with a ceremony involving the greeting-face, nose-sniffing, rubbing, and smelling of the genitals, ending with an incipient threat-jump. Young or weak stallions respond to approach with the estrous face, as shown by a mare before or during copulation.

Group members search for, and are sought by the group if lost. One adult guards the group when at rest. Group members other than the dam will wake juveniles in imminent danger. Zebras defend themselves against cheetahs, wild dogs, and hyenas, but not lions, by kicking or biting. When a family is attacked, the stallion takes the offensive.

The family stallion is the alpha-dominant within the group, foals have the rank of their dam, and rank-order is maintained in single-file movements, though the dominant female usually leads. Stallion-group adults are apparently of equal rank, but there is a dominance hierarchy among the adolescents. Group males will urinate or defecate over the deposits of others.

In Ngorongoro, family groups include one to six mares, with the stallion and foals making up to 15 members (Klingel, 1965a). Mean family size was 7.7 in Ngorongoro, 5.4 at Rukwa, 5.1 in the Serengeti, 4.7 at Etosha and 4.6 at Wankie (Klingel, 1967). In the Kruger National Park, family size ranges from 2 to 11, with a mode of 4 and a mean of 4.0 to 4.5 (Smuts, 1976c). It is lowest where estimates of grass height, thicket density, and predator-kill indices are all highest. Monfort and Monfort (1978) give a mean family size of 7.1 (3 to 14, mode 7) for the Akagera Park, Rwanda.

Stallion groups included up to 15 animals at Ngorongoro (Klingel, 1965a) and one to seven, with a mode of two or more usually three, at the Kruger National Park (Smuts, 1976a).

The male sniffs the urine or feces of estrous females and then may show flehmen, followed by urinating or defecating on the deposits of the female. Precopulatory grooming of young mares occurs, with copulation only on the third or fourth day of estrus. There is little or no precopulatory activity with adult mares, which are mounted repeatedly during the whole of estrus, but with intromission every one to three hours only at the height of estrus (Klingel, 1969a; Trumler, 1956).

Combat over young mares in estrus is not ritualized, and involves running, circling, neck-wrestling, biting from standing and sitting positions, and kicking (Backhaus, 1960a, 1960b; Estes, 1967; Klingel, 1967). Klingel (1967) recorded no submissive behavior but Backhaus (1960b) reported that the winner laid its head on the loser's rump as if preliminary to mounting.

GENETICS. A possible hybrid of *E. grevyi* × *E. burchelli* in nature was reported by Keast (1965). Otherwise, hybrids between *E. burchelli* and other equids have only been obtained in captivity. The literature on hybrids between *E. burchelli* and *E. caballus*, *E. asinus*, *E. hemionus* or *E. zebra* was reviewed by Gray (1972). Hybridization with *E. grevyi* was reported by Benirschke (1977) and Ryder et al. (1978). With horse or ass as parent, striping in the hybrid is variously developed, tending to be narrower than in the *E. burchelli* parent (see especially Ewart, 1899). Male hybrids are sterile as there are either no spermatozoa in the testis or ejaculate, or if present, they are abnormal. Spermatogenesis is blocked at the late pachytene stage. Females, however, can be fertile, though no back-crosses have been reported. In hybridization with other species of zebra the striping of hybrids is intermediate in pattern between those of the parents. A *E. grevyi* × *E. burchelli* hybrid superficially resembles *E. zebra*. Striping is complete down to the hooves even when the *E. burchelli* parent has white shanks and pasterns. The fertility of these hybrids has not been reported.

The diploid chromosome number of Burchell's zebra is 44. There are 17 pairs of metacentric and 4 pairs of acrocentric autosomes. The X chromosome is submetacentric, and the Y is a minute, possibly acrocentric, chromosome. The subspecies *E. b.*

boehmi and *E. b. antiquorum* from Namibia and Transvaal have identical unbanded karyotypes (Benirschke et al., 1963; Heinichen, 1969; Hsu and Benirschke, 1971). The total number of chromosome arms (at least in females) is 80, as in Grevy's zebra, but differs from all other equids. By comparison with Grevy's zebra, Burchell's zebra has an additional pair of metacentric chromosomes, but lacks two pairs of acrocentric chromosomes, suggestive of a Robertsonian fusion. This tallies with the view that *E. grevyi* has the more primitive morphology (Groves, 1974). However, not all pairs are perfectly homologous, for in a male *grevyi* × *burchelli* hybrid, with $2n = 45$ and with three elements unpaired as expected, the chromosomes were not identical in two of the apparent pairs (Benirschke, 1977; Ryder et al., 1978).

REMARKS. Burchell's zebra and the quagga have been regarded as separate, formerly partly sympatric species (Ansell, 1971; Gentry, 1975; Groves, 1974). However, there is considerable variation in the striping pattern of the quagga, and supposedly diagnostic features of the pelage are seen at least in incipient form in specimens of *E. b. burchelli* (Rau, 1974, 1978). Some specimens of nominate *burchelli* in turn closely approach the more heavily striped *quagga* specimens (Antonius, 1951; Gregory, 1926; Lyon, 1907), so the likelihood that there was once a zone of intergradation between the two taxa seems quite high. The differences in skull proportions between the two species, reported most recently by Gentry (1975), and the specific status of the two forms, require thorough re-evaluation.

There is some uncertainty concerning the distinctiveness of the southern subspecies of Burchell's zebra, for individuals conforming with the type of one subspecies may be found within the range of another. For instance, animals which are typologically *E. b. burchelli* appear in Etosha and Zululand *antiquorum* populations (Franz, 1956; Rau, 1978), though *E. b. burchelli*, as a subspecies, is extinct. Cabrera (1936) included *chapmanni* in *antiquorum*, while Rzańnicki (1951) placed *antiquorum* in *burchelli*. Kingdon (1979) concluded that populations of zebras were isolated by swamp and forest in savanna refuges during the late Pleistocene and that subsequently they intergraded, *zambeziensis* representing *boehmi-craushayi* intergrades, and *chapmanni* and *antiquorum*, *craushayi-burchelli* intergrades.

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